Life history and foraging ecology of muricid gastropod Cronia margariticola(Dissertation_全文)

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Life history of the muricid gastropod, Cronia margariticola (Broderip, 1833): growth mode transition with season and sexual maturity

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Abstract: Growth mode, foraging activities and reproductive characteristics of Cronia margariticola (Gastropoda: Muricidae) were investigated in the rocky intertidal seashore of Shirahama, Wakayama, Japan. C. margariticola, which reached sexual maturity at about 16 mm in shell height, was found to have a distinct annual reproductive cycle. Mounting was frequent in May and June, and oviposition, primarily into beds of the mussel Hormomya mutabilis, took place during June and July. Egg size (0.16-0.21 mm in diameter) suggested that C. margariticola hatch at the planktonic stage. Feeding was observed from April through October, but was restrained during the peak reproductive season. Monthly size distribution showed that the settled population appeared in August. Mark-recaptured samplings revealed that juveniles continued growing from March through January, taking 1 to 2 years to reach adult size. In contrast, adults grew from July through January, allocating energy obtained by feeding for reproduction in the spring and for growth in the fall. Analysis of adult growth indicated that growth rate was inversely related to whelk size. Using the von Bertalanffy model with compensation for size decrement due to shell attrition, growth simulation suggested that the presumptive mean life expectancy of C. margariticola in

this location was 7 to 8 years.

Key words: Cronia margariticola, Muricidae, growth, reproduction, tidepool

INTRODUCTION

Cronia margariticola (Broderip 1833), which belongs to the family Muricidae, is a native of the rocky intertidal seashore along the northern Indo-Pacific Ocean (Tsuchiya 2000). In contrast to most muricids, which are generally considered active hunting carnivores (Carriker 1981; Hughes 1986), C. margariticola is a facultative hunter and carrion feeder (Abe 1980; Keable 1995; Tsuchiya 2000). Recently at Shirahama, Wakayama, in the south-western part of Honshu, Japan, C. margariticola was observed to kleptoparasitize or scavenge food from the valve aperture of mussels just fed on by other muricids or from a hole drilled by the initial predator (Ishida 2001), suggesting that there are strong interspecific relationships between C. margariticola and other muricids.

Due to the presence of the warm Kuroshio current, diverse marine animals, including muricid gastropods, inhabit the Pacific coast of the southern Japanese Islands (Nishimura 1992). At least eight muricid species have been found at Shirahama (Ishida & Iwasaki 1999), suggesting the coexistence of muricids belonging to the same

trophic level (Abe 1989; Yamamoto 1997). To analyze the mechanism and dynamics of communities containing diverse species, it is important to determine the life history of each constituent species. In benthic communities, it has been shown that characteristics of reproductive activity (Turra & Leite 2000; Stead et al. 2002), foraging (Ota & Tokeshi 2000; Gaymer et al. 2001), and growth (Laura 2000; Turra & Leite 2001) are strongly related to interspecific interactions and coexistence. This information, however, is not yet known for muricid species along the Pacific coast of Japan. We therefore sought to determine the life history of C. margariticola. Monthly quadrate samplings and mark-recapture growth measurements of C. margariticola at Shirahama were made in order to analyze the seasonal and body-size dependent growth of this species. In addition, its foraging and reproductive activity were observed in order to determine how this species integrates resource allocation into its growth strategy.

MATERIALS AND METHODS

Study Site

Field sampling was carried out in a tidepool (for tidepool characteristics, see Ishida (2001)) on a moderately wave-exposed rocky shore near the Seto Marine Biological Laboratory of Kyoto University (SMBL), Shirahama, Wakayama, Japan (33°41'N, 135°21'E). Laboratory experiments were carried out at SMBL.

Size distribution

To construct the size distribution of C. margariticola in the field, the shell height of all individuals found in the quadrat established in the study tidepool was measured. Samplings were made once every month from April to August 1998 and from April 1999 to February 2000, except for June 1999, November 1999 and January 2000. A 5 m^2 study quadrat was set up on the tidepool substratum each month, with the exceptions of April and May 1998, for which the quadrats were 3.5 m^2 and 4.5 m^2, respectively. Shell height, defined as the distance from the apex to the tip of the anterior siphonal

canal, were measured to the nearest 0.1 mm with vernier calipers.

During sampling, the state (resting, breeding or feeding) of each C. margariticola was recorded. Breeding was defined as being either part of a mounting pair or an ovipositing individual. Typical mounting was defined as one individual attached to the suture of the other one. In some mounting pairs, copulation was actually observed;, i.e., the top individual had extended its penis and inserted it into the aperture of the bottom one. Ovipositing behavior was not distinguished during samplings in 1998, but was recorded in April 1999 and thereafter.

Feeding was defined as drilling, ingesting or just clustering around other ingesting whelks. Because details of C. margariticola feeding ecology have been described previously (Ishida, 2001), only the percentage of feeding individuals for each month is reported here.

Laboratory observation for oviposition

To measure the size and potential number of eggs laid by an individual C. margariticola, animals were induced to lay eggs in the laboratory. Each of 32 muricids was

individually placed in a 1.4 L plastic aquarium for 40 days, along with sufficient prey mussels of the species Hormomya mutabilis. Running seawater was supplied and allowed to overflow from the aquarium lids. Experiments were performed twice, from June to July 1998 and July to August 1998.

Growth measurement by the mark-recapture method

To analyze the seasonal growth of C. margariticola in the field, a mark and recapture observation was made once per month from August 1997 to August 1998. In August 1997, 108 individuals of C. margariticola (shell height, 11.7–25.1 mm) were collected from the study tidepool. Each muricid was tagged with a lettered plastic tape (DYMO Corp.), weighing less than 6% of the weight of each muricid, glued onto its shell with epoxy resin. The height of each shell was measured with vernier calipers to the nearest 0.1 mm, and the muricids were released into the study tidepool.

Tagged muricids were recaptured once every month, except for December 1997, during the day at spring low tide level, and the shell height of each was measured. Each collected muricid was again released into the study tidepool within 2 days of

capture and measurement.

In September and October 1997 and February and May 1998, additional muricids were tagged and released (Table 1). These animals were undercoated on their shell surface with white enamel paint, tagged by numbering them with carbon ink, and overcoated with cyanoacrylate glue. The weight increment of this tagging was < 6% of each muricid wet weight.

Tab1

Shell height increments over each 30 day period were calculated for muricids recaptured at successive samplings, after correcting for the actual sampling intervals. If a muricid was not recaptured after 1 month but was recaptured after 2 months, the shell height of the intervening month was assumed to be the median of the two measurements.

RESULTS

Reproduction of C. margariticola

The great majority of breeding C. margariticola sampled, whether mounting or ovipositing, were found to have shell heights greater than 16 mm (Figure 1). Only 6/193 (3.1%) of breeding muricids were smaller than 16 mm, 5/151 (3.3%) of the mounting muricids and 1/42 (2.4%) ovipositing muricids.

Fig1

C. margariticola has a distinct annual reproductive cycle. Mounting was frequent in May and June, and ovipositing reached a peak in June and July (Figure 2). Observed breeding muricids included marked individuals, and it was noted that males engaged in multiple copulations during one breeding season. It was unclear, however, if females also engaged in multiple copulations.

Fig2

In most cases oviposition was made on beds of the mussel, H. mutabilis. C. margariticola extended and inserted the forepart of its foot in a gap between mussels, pressed its foot, and laid egg capsules onto the H. mutabilis shell surface, which was sheltered from the bed exterior (Figure 3). In 1/45 (2.2%) ovipositions, C. margariticola laid eggs in the hollow of a rock substratum. No remarkable aggregations were observed during egglaying.

In the laboratory, eight C. margariticola laid 5-104 capsules each (mean, 51.8±30.9SD capsules). Each capsule, which was transparent and had a lenticular shape about 2.0-2.5 mm in diameter with a hatching out hole at the center, usually contained about 80-100 eggs each, with each of the latter being about 0.16-0.21 mm in diameter. During egglaying in the laboratory, C. margariticola inserted its foot into a slit in the aquarium lid and laid eggs between the slits or on the outside of the aquarium.

Fig3

Feeding activity of C. margariticola

Feeding C. margariticola were observed from April to August 1998 and April to October 1999 (Figure 2). Feeding activity was restrained from June to July, coincident with the peak egglaying season. No feeding C. margariticola was observed from December to February 1999.

Size Histogram

Figure 4 shows the shell height distribution of C. margariticola obtained from 13 observations between April 1998 and February 2000. The settled population appeared

in August. Two major populations, divided between those larger or smaller than 16-18 mm in shell height, were observed from August through April. The mode of the smaller shell height population shifted and was included in the larger shell height population over time, whereas the larger mode was almost static around 20-22 mm. The number of smaller individuals is considerably less than that of the larger individuals, suggesting that the growth rate slows when C. margariticola reaches 16 mm in shell height.

Fig4

The observed maximum shell height was 26 mm. It is difficult to distinguish the yearly cohorts from these size histograms.

Seasonal growth rate

The average monthly recapture rate was about 50% and never went below 34% per month (Table 1). Shell height and incremental growth over each 30-day period for mark-recaptured individuals were plotted for each month (Figure 5). These results showed that muricids smaller than about 16 mm continued to grow from March through January. In contrast, muricids larger than 16 mm grew from July through January; and

there were negative relationships between shell height and each 30-day increment during their growing season. For all muricids, shell height decreased during the non-growing season, probably because of shell attrition.

Fig5

Individual muricids were separated into two stages, juveniles (<16 mm) and adults (≥ 16 mm), to consider the growth pattern of each. Juvenile size history was obtained from mark-recaptured data of 11 individuals, which were smaller than 16 mm when originally marked (Figure 6). Individuals having a shell height of 10 mm during the winter were found to grow to > 14 mm by the following summer, and were expected to grow to > 16 mm by the second summer. The size histogram data indicates that the settled season of these individuals is relatively late. In contrast, earlier settled individuals, which were about 14 mm during the winter, were expected to grow to 16 mm by the following summer.

Fig6

To simulate the growth of adults, the von Bertalanffy (VB) model (von Bertalanffy 1938) was applied. Differentiation of the VB growth function over time resulted in the equation:

$$\frac{dH}{dt} = K(H_{max} - H)$$

where H = shell height (mm), H_{max} = maximum shell height (mm) and K = growth coefficient (constant). This equation shows that the relationship between the instantaneous growth rate and the present size represents a negative linear correlation, which intersects the x-axis at H_{max}. This led to the correlation equation,

$$g(H_i) = a(H_{max} - H_i) \qquad (1)$$

where H_i = shell height at the beginning of month i (mm), $g(H_i)$ = shell height increment per 30 days of month i and a = correlation coefficients, minimizing the residual sum of squares for each month. Because observed growth data may be an underestimate due to shell attrition, each monthly shell increment was compensated by adding the mean value of monthly decrement, calculated from the January-February to May-June data sets (0.053 ± 0.072SD mm), during which time almost all of the individuals were considered to suspend growth. Maximum shell height (H_{max}) was taken as 26 mm,

the observed maximum shell height.

The results of explored correlation coefficients (a) and of testing the significance of each estimate of regression are shown in Table 2. Significant correlation was found in the September-October, October-November, November-(December)-January and July-August data sets, while correlation in August-September was marginally significant ($p = 0.098$; Table 2). Significant regression lines are drawn in Figure 5.

Tab2

The growth of adult C. margariticola was simulated using the equation:

$$H_{i+1} = H_i + g(H_i) - D$$

where D = mean monthly decrement by shell attrition (i.e., $D = 0.053$), $g(H_i)$ is equivalent to that in Equation 1 during the growing season (i.e., from July through January) and $g(H_i) = 0$ during the non-growing season (i.e., from January through July). From November to January, growth was simulated by repeating the November-(December)-January growth twice. This simulation indicates that a muricid of shell height 16 mm in April needs 6 years to achieve a shell height of 21 mm (Figure 7). In

this simulation, the growth rate decelerates rapidly after a muricid achieves a shell height of about 22 mm. As a result, it took 26 years to achieve 23 mm, and the height did not exceed 23.1 mm during a very long period of time (50-100 years).

Fig7

DISCUSSION

This study has revealed basic information about the reproductive ecology of C. margariticola. Mounting for copulation usually commenced in April and was frequent during May and June. Peak oviposition occurred subsequently, during June and July. C. margariticola laid its eggs primarily on the shell surface of the mussel, H. mutabilis, which was sheltered from the bed exterior. Ovipositing behavior observed in the laboratory (i.e. laying eggs outside the aquarium through the slit) was essentially similar to that in the field. These observations suggest that, by laying eggs in protected areas, C. margariticola acts to avoid egg predation.

Laying of eggs in aggregations has been observed in other species of muricids,

including the genus Thais (Chari 1950; Amio 1963; D'Asaro 1966; Spight 1974; Nakano et al. 1981), and is considered another effective strategy for avoiding egg predation (Abe 1983). In contrast, breeding aggregations were not observed in C. margariticola. The present observations suggest that, instead of breeding aggregations, C. margariticola avoids egg predation by carefully choosing the egg-laying space. The observed egg capsule shape, size and egg-laying sites of C. margariticola are similar to those of the related species, Ergalatax contractus (Habe 1960).

Although egg development and hatching of C. margariticola were not observed directly, the size of the eggs (0.15-0.20 mm in diameter) suggests that they hatch out at planktonic larval (i.e., veliger) stage. Most marine gastropods that hatch out at the veliger stage usually lay eggs smaller than 0.3 mm in diameter (Amio 1963). Size histograms for C. margariticola showed that, for this species, first recruitment occurred in August, with the hatched larvae settling and growing to 8-10 mm in shell height from July through September.

Most C. margariticola engaging in reproductive activity were larger than 16 mm, suggesting that this is the minimum size for sexual maturity and confirming findings

from an anatomical analysis (Fujioka 1984). The growth mode of C. margariticola also switched after reaching around 16 mm in shell height, with size histograms indicating that growth rate decelerated after this point. Growth analysis from mark-recapture data showed two growth stages, with juveniles (< 16 mm in shell height) showing continuous growth from March through January and adults (> 16 mm in shell height) growing from July through January. During the winter, both juvenile and adult C. margariticola showed decelerated growth rate, as well as refraining from foraging, suggesting that growth suspension is caused by a reduction in metabolic rate associated with low temperatures. In contrast to juvenile C. margariticola, adults of this species showed a suspension of growth from April to June, although they fed actively during this time, and especially during April and May. Since this season coincided with the beginning of the reproductive period, the suspension of growth by adults during this time period was probably due to increased reproductive activity. That is, the energy obtained from feeding during this season seemed to be preferentially invested in reproduction rather than growth, e.g., in gametogenesis, copulation and mate guarding. Similar results have been observed in other muricids, e.g., Morula musiva in Hong

Kong (Tong 1986).

From the size histograms, it was difficult to distinguish the mode of annual recruitment in the adult population, making it necessary to run a growth simulation from the monthly adult growth data. This simulation revealed that it would take about 6 years for a 16 mm individual to grow to 21 mm, which is the size mode of the adult population. In addition, some mark-recapture data of juveniles and the results of the size histograms indicated that it would take 1 to 2 years for settled C. margariticola to achieve adult size (> 16 mm). Therefore, the presumptive mean life expectancy of C. margariticola would be 7 to 8 years in this locality. This is similar to the life expectancies of other intertidal muricids, e.g., Thais clavigera (7 years) and Morula musiva (9 years) in Hong Kong (Tong 1986).

The growth simulation, however, did not exactly fit the size histogram data. For example, the simulation indicated that it would take more than 26 years for adults to exceed 23 mm in shell length, and that they would not exceed 23.1 mm even after 50-100 years. In contrast, the size histogram data showed that the number of individuals exceeding 23 mm in shell height accounted for about 10% of the C. margariticola

population. This discrepancy may be due to the growth correction for continuous shell attrition included in the simulation. This simulation assumed that the decrease in shell height was directly, and linearly, proportional to time. The coefficient used, 0.053 mm/30 days, which was calculated as the mean decrement during the winter season, had a large variance (SD = 0.072). It is likely that C. margariticola residing in areas sheltered from wave erosion, such as crevices, might not lose shell and might grow more than calculated by the simulation. Few studies, however, have analyzed molluscan growth while considering shell attrition, suggesting the need for more observations of other intertidal species to arrive at a more accurate growth simulation model.

While the results of this study have indicated that growth mode transition in C. margariticola is associated with reproductive activity, confirmation requires the ability to distinguish the sexes. For example, the energy cost of gametogenesis will be different between males and females, in that the production of eggs is usually more costly energetically than that of sperm. Other reproductive behavior, including mate search and mate guarding pre- or post-copulation, will have different energy costs

between the sexes. The copulation method of C. margariticola would also affect its foraging activity. For example, while it is impossible for males to drill or ingest mussels while mounting, females can prey on mussels while being mounted and even during copulation (Ishida, personal observation).

This intersexual asymmetry in energy flow during reproduction may affect the growth mode. In the present study, growth data did not distinguish between the sexes because there was no sexual dimorphism in shell morphology of C. margariticola. In future, individuals can be sexually identified and marked by their behavior during the reproductive season, including mounting, copulating or ovipositing, and their subsequent growth can be measured to determine if there is any intersexual asymmetry in growth mode.

It is also important to estimate the exact cost of reproductive activity for each sex. For example, by quantifying the metabolic expenditure required for growth and reproduction (Bayne & Newell 1983), the energy allocation mechanism could be determined (Stickle & Bayne 1987; Navarro et al. 2002). Integration of more precise data may reveal the energy allocation strategy in C. margariticola and would contribute

to the general understanding of molluscan growth ecology. In addition, these basic life history parameters would be fundamental in analyzing multispecific interactions and coexistence ecology.

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TABLES

Table 1. Monthly record of released and recaptured C. margariticola individuals. Cumulative total release and recapture rates are calculated for each month. Monthly growth plots were increased by interpolation and generated plot numbers are also shown. For details of this procedure, see text.

	Cumulative Total Released	Additional Released	Recaptured	Recapture Rate (%)	Interporated Plots
Aug.97	108	-	-	-	-
Sep.97	108	3	71	65.7	4
Oct.97	111	18	58	52.3	7
Nov.97	129	0	77	59.7	4
Jan.98	129	0	57	44.2	7
Feb.98	129	30	51	39.5	17
Mar.98	159	0	99	62.3	9
Apr.98	159	3	97	61.0	9
May.98	162	0	83	51.2	12
Jun.98	162	0	75	46.3	5
Jul.98	162	0	60	37.0	7
Aug.98	162	0	55	34.0	-
Mean±1SD				50.3±11.0	
Total					81

Table 2. Correlation coefficients (a), sample number (n), and F and p values for testing the significance of each estimate of regression. The results of the April-May and May-June data sets are not shown, because each a was negative.

	a	n	F	p
Aug-Sep	0.0410	73	2.818	0.0976
Sep-Oct	0.0696	60	13.277	0.0006
Oct-Nov	0.0206	74	6.849	0.0108
Nov-(Dec)-Jan	0.0050	57	4.261	0.0437
Jan-Feb	0.0055	59	1.543	0.2193
Feb-Mar	0.0044	85	2.714	0.1033
Mar-Apr	0.0025	96	0.542	0.4634
Apr-May	-	93	-	-
May-Jun	-	76	-	-
Jun-Jul	0.0003	64	0.001	0.9703
Jul-Aug	0.0582	48	4.055	0.0499

Figure captions

Fig 1. Shell height plots of mounting (a) and ovipositing (b) C. margariticola. Each bar represents the mean (middle line) ±1SD (top and bottom ends).

Fig 2. Percentage of C. margariticola individuals observed in mounting, ovipositing and feeding behavior during each month.

Fig 3. Egg capsules of C. margariticola laid on the mussel H. mutabilis (formalin fixed specimen; shell length = 21 mm). Most capsules were laid on sheltered areas. The area was visible because white coralline algae had not been uncovered (solid line).

Fig 4. Frequency distributions of C. margariticola shell heights. Muricids were sampled during 13 monthly observations from April 1998 to February 2000. Sample number is shown under each month.

Fig 5. Shell heights and 30 day increments obtained from monthly mark-recaptured C. margariticola individuals (solid circles ≥ 16 mm; open circles < 16 mm in shell height). Horizontal broken lines represent y = -0.053, i.e., the mean monthly shell height decrement by attrition. Significant growth correlation lines assuming the VB model were drawn, with a downward shift along the y-axis (-0.053) to fit the original plots that did not compensate for decrements due to shell attrition. The maximum shell height (x = 26) is indicated by a solid triangle for each month.

Fig 6. Size history of juvenile (< 16 mm shell height) C. margariticola obtained from mark-recaptured data of 11 individuals.

Fig 7. Growth simulation of adult (≥ 16 mm shell height) C. margariticola. Simulation was started at 16 mm shell height in April and run for 12 years. The left end of each growth plot continues from the right end of the previous plot.

日本語要旨

和歌山県白浜町の岩礁潮間帯において、アクキガイ科腹足類ウネレイシガイダマシ *Cronia margariticola* の成長様式、摂食活動および繁殖生態について調べた。ウネレイシガイダマシは殻高およそ16ミリで性成熟し、5月から6月にマウンティング、6月から7月に産卵のピークを迎える年1回の繁殖周期を示した。卵嚢はヒバリガイモドキ *Hormomya mutabilis* のベッド内に産みこまれ、卵サイズ（直径0.16-0.21mm）から浮遊幼生段階で孵化するものと推定された。摂食活動は4月から10月まで観察されたが、繁殖ピーク時には抑制されていた。月ごとのサイズ頻度分布では、着底個体の加入は8月に認められた。標識再捕による成長解析では、未成熟個体は3月から次の1月まで成長を続け、成熟サイズに達するのに1年から2年を要すると考えられた。一方成熟個体の成長は7月から次の1月までで、春の摂食で得たエネルギーは繁殖へ、秋のエネルギーは成長へ主に投資していると考えられた。成熟個体の成長解析によると、体サイズと時間当たり成長量は負の相関を示した。殻の摩耗量で補正したフォン・ベルタランフィ成長モデルに基づく成長シミュレーションの結果、平均寿命は7-8年と推定された。

FIGURES

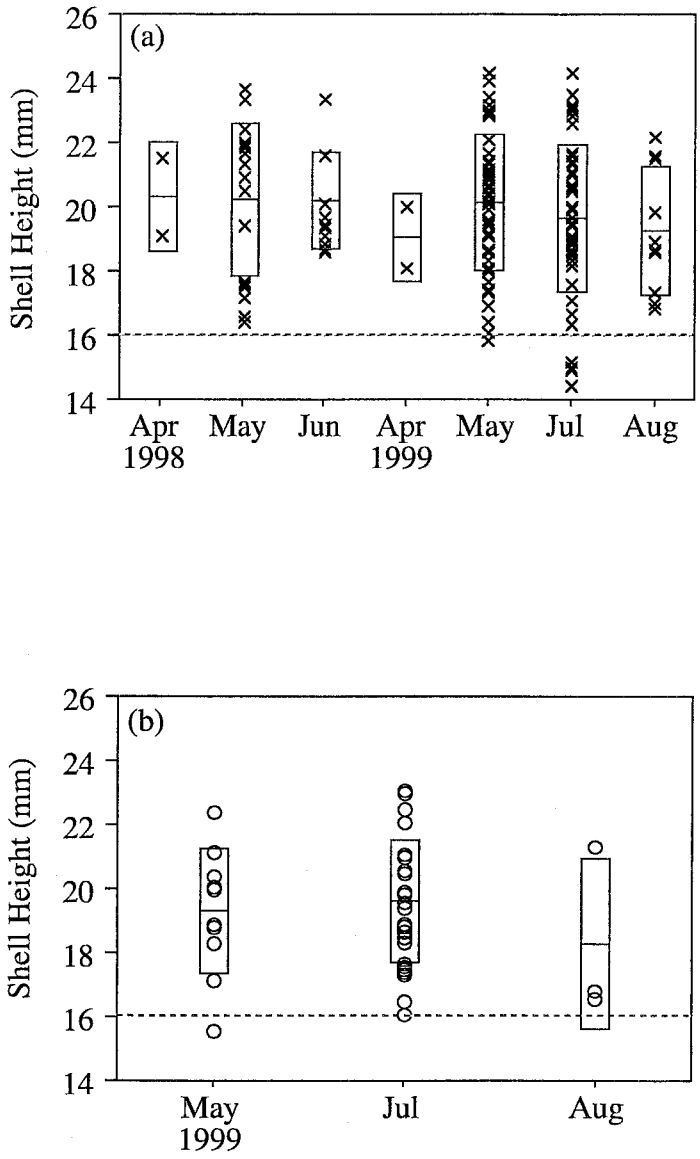

Figure 1

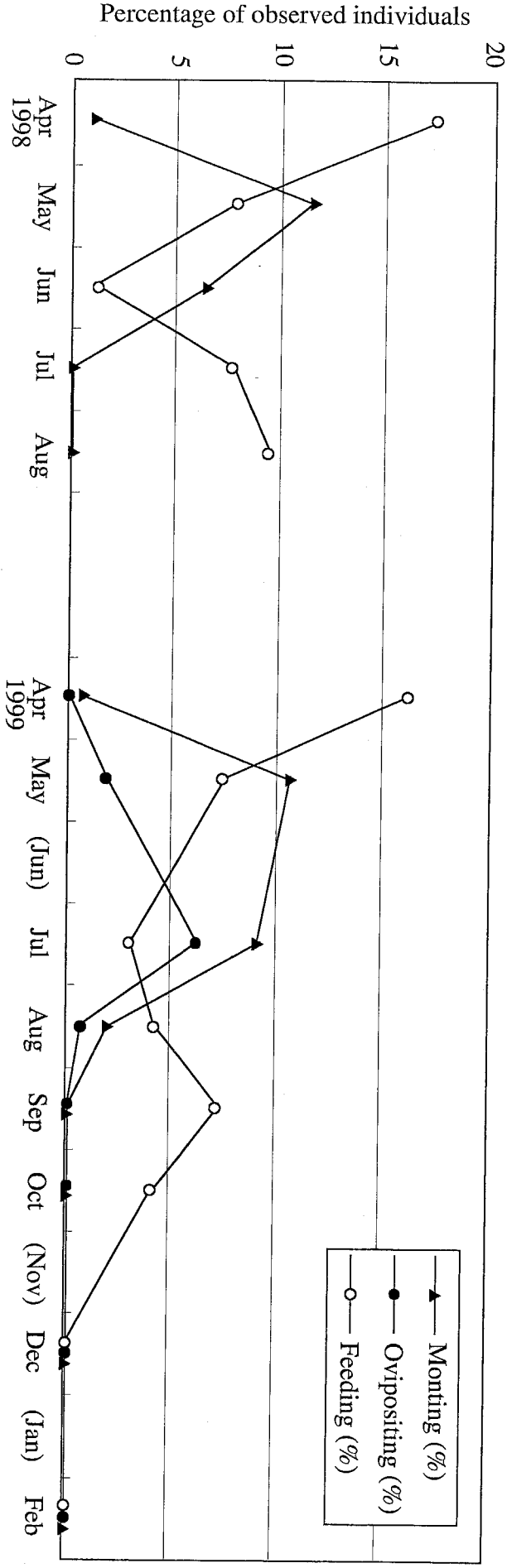
Percentage of observed individuals
0
5
10
15
20
Apr 1998
May
Jun
Jul
Aug
Apr 1999
May
(Jun)
Jul
Aug
Sep
Oct
(Nov)
Dec
(Jan)
Feb
Monting (%)
Ovipositing (%)
Feeding (%)

Figure 2

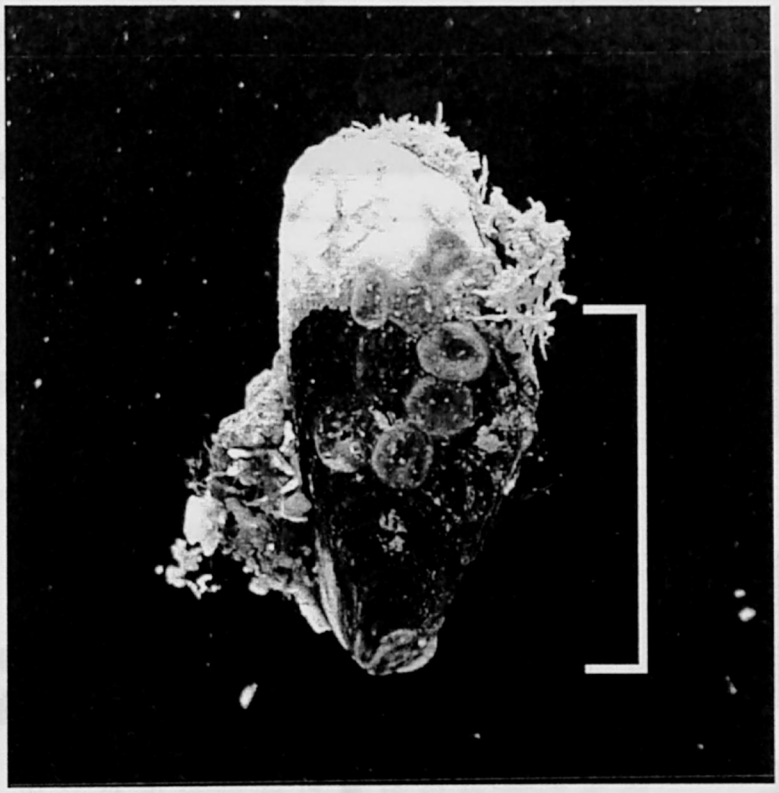

Figure 3

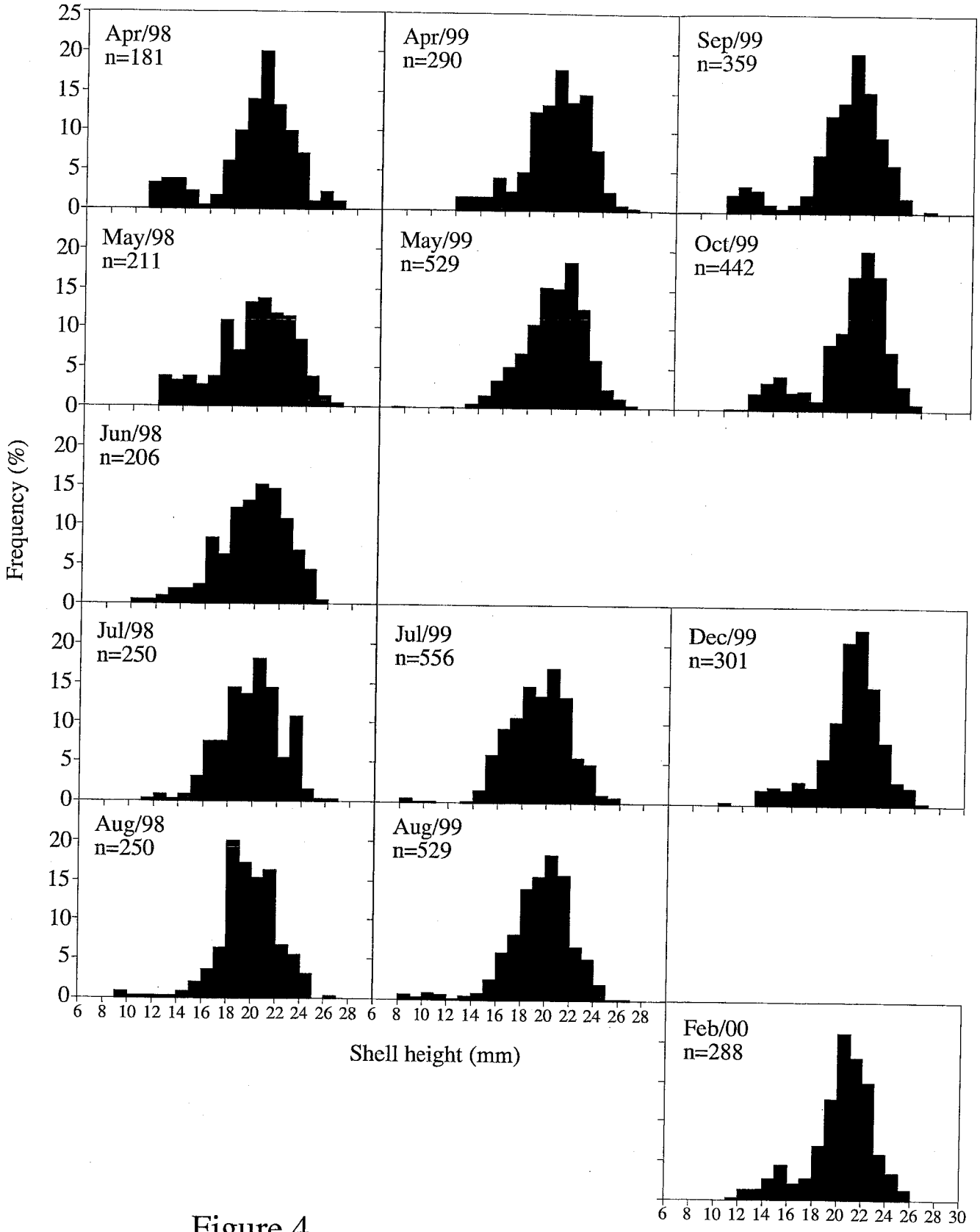
Apr/98
n=181
Apr/99
n=290
Sep/99
n=359
May/98
n=211
May/99
n=529
Oct/99
n=442
Jun/98
n=206
Jul/98
n=250
Jul/99
n=556
Dec/99
n=301
Aug/98
n=250
Aug/99
n=529
Feb/00
n=288
Frequency (%)
Shell height (mm)

Figure 4

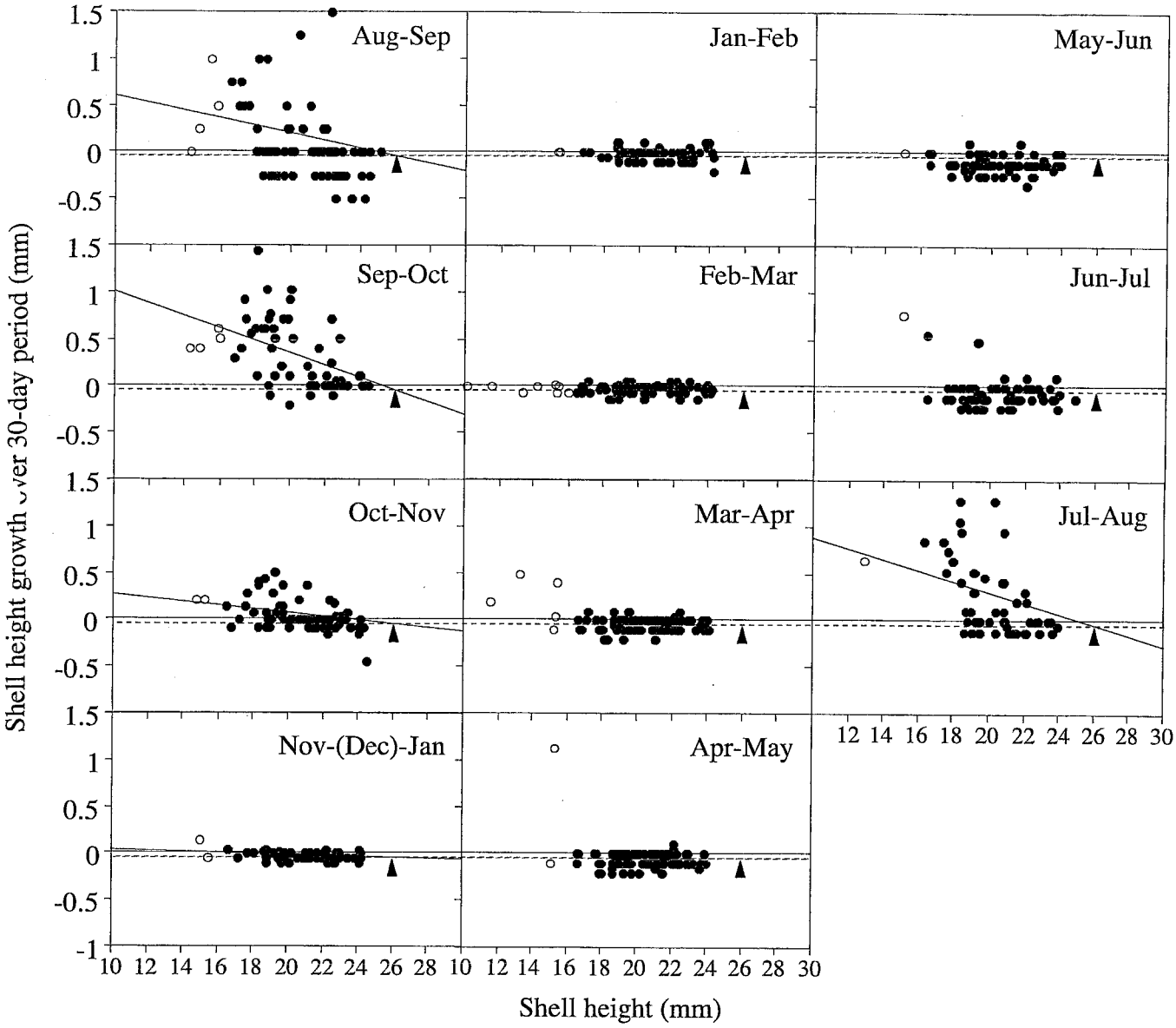
Aug-Sep
Jan-Feb
May-Jun
Sep-Oct
Feb-Mar
Jun-Jul
Oct-Nov
Mar-Apr
Jul-Aug
Nov-(Dec)-Jan
Apr-May
Shell height growth over 30-day period (mm)
Shell height (mm)

Figure 5

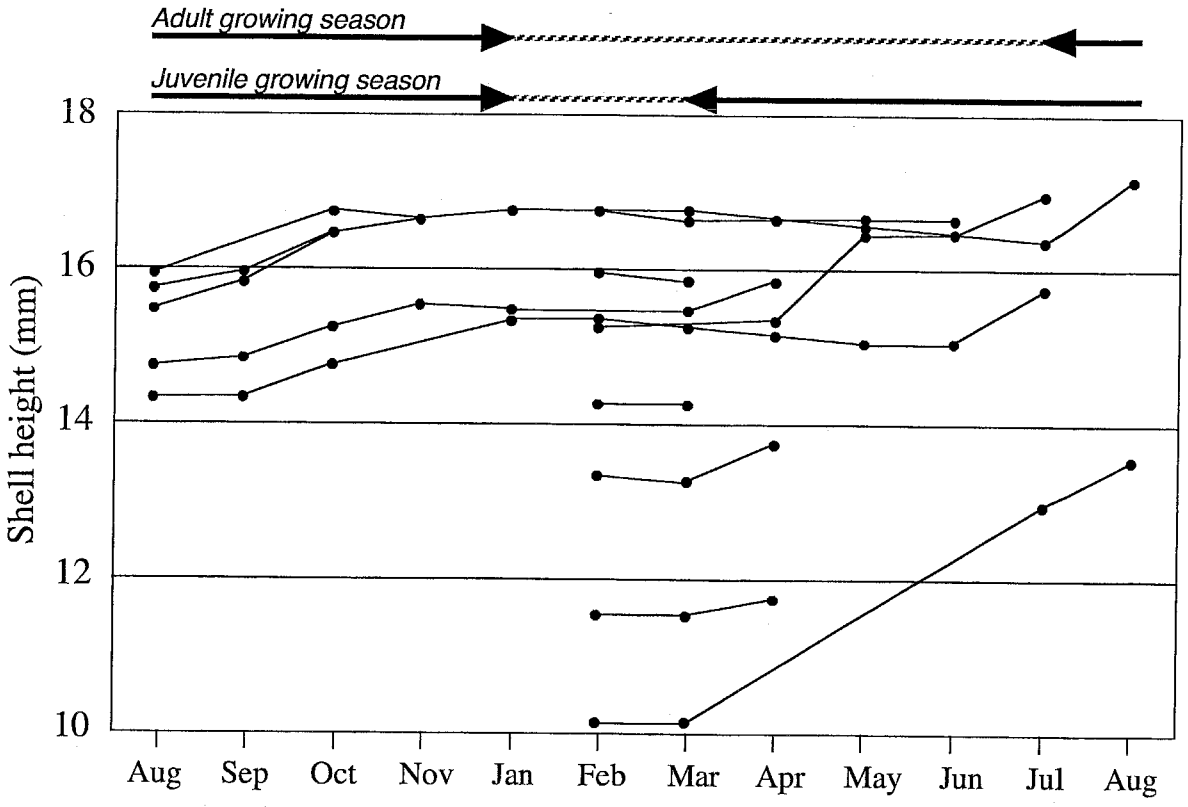
Adult growing season
Juvenile growing season
Shell height (mm)
18
16
14
12
10
Aug
Sep
Oct
Nov
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug

Figure 6

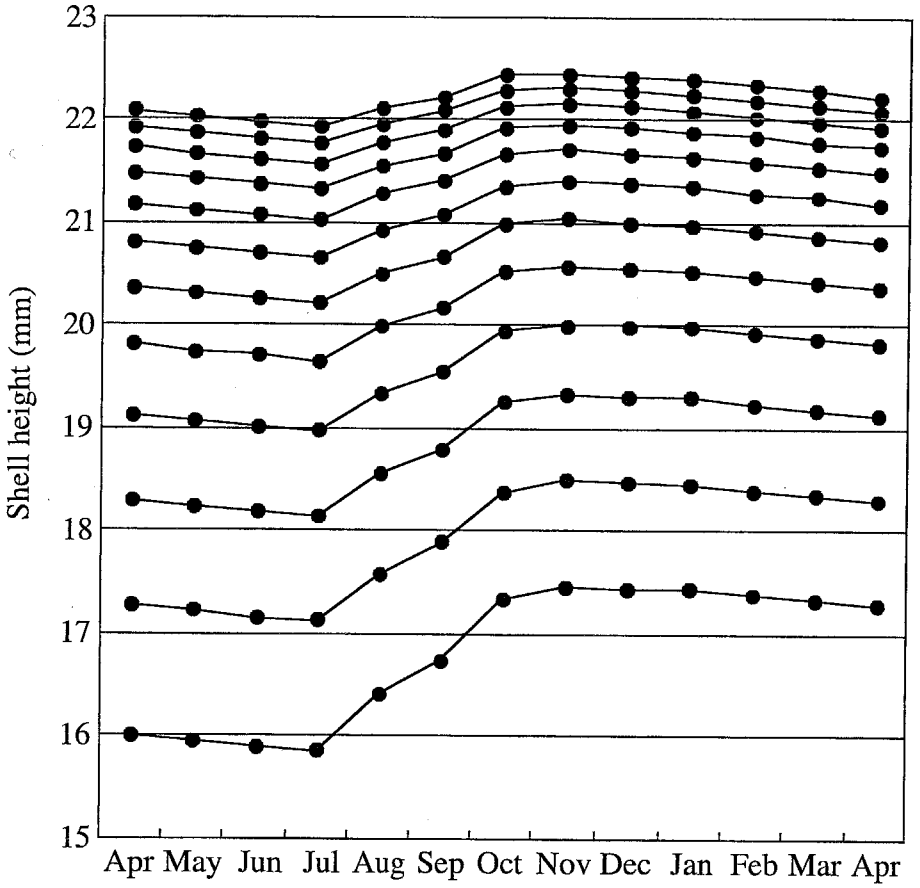
Shell height (mm)
23
22
21
20
19
18
17
16
15
Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr

Figure 7